ACCUMULATION AND DISCHARGE OF SPAWN BY OYSTERS LIVING AT DIFFERENT DEPTHS

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Introduction

While conducting studies on the biology of the oyster, *Ostrea virginica*, of Long Island Sound, an opportunity presented itself to observe and compare the condition of the gonads of these animals living at different depths. Such a study is of interest since the literature does not offer any comparative data pertaining to the accumulation of spawn and spawning activities of oysters existing in shallow and deep water. There are in the literature, however, several references which indicate that the oysters of shallow water discharge their spawn earlier than those of deep water. For example, Churchill (1920) states that the spawning period of *O. virginica* is regulated by the depth of the water and the general meteorological conditions. Nelson (1928), working in New Jersey, also expressed the opinion that oysters in shallow water spawn before those in greater depth. Neither of the two above-mentioned investigators, nor other workers making similar statements, offered any comparative data in support of their observations. Furthermore, no suggestion was offered as to what should be considered as shallow or deep water.

In Long Island Sound very shallow waters are not suitable for oyster cultivation because wave action during storms may shift and often destroy the oysters. On the other hand it becomes increasingly difficult to cultivate the beds and take care of the oysters in waters deeper than 30 or 35 feet. As a result of these conditions the greater part of the oyster grounds of Long Island Sound is confined to the depths ranging from 10 to 30 feet. Therefore, in these studies it was decided to confine observations to the same depth range.

Methods

These studies were conducted in the summer of 1941. There were 14 sampling stations established in the oyster-growing area confined between Bridgeport and New Haven harbors. Of this number, four stations were located at a 10-foot depth, six stations at a 20-foot depth,

and four stations at a 30-foot depth. It is proposed to regard the above mentioned groups of stations as shallow, medium deep, and deep, respectively.

The collection of samples for observations on the average thickness of the gonadal layer of oysters living at the three different depths was begun on June 11 and continued until September 3. At each station a dredge-load of oysters was brought up and a sample of ten adult animals of four or five years of age was taken from it at random. Thus, 140 individuals were examined on each trip. The body of each oyster was cut transversely on the right side along a line extending through the stomach on a level with the lower edge of the palps, and the thickness of the gonadal layer was measured with a caliper. To determine the time of the beginning of spawning of the oyster population, numerous other samples were taken at very frequent intervals during the early part of July.

Several days after the beginning of spawning, collection of additional samples of oysters for determination of the condition of their gonads was initiated. Each sample now consisted of 20 individuals: thus during each trip 280 oysters were collected from 14 stations. The oysters were opened, dissected, and the condition of their gonads determined. On the basis of such an examination the oysters were classified as ripe-but-unspawned, less-than-half spawned, more-than-half spawned, and completely spawned.

Observations

The first measurements of the gonads of oysters made on June 11 showed that the gonadal layer was very thin and that the majority of the animals was unripe. Oysters of the shallow stations were the most advanced, the mean thickness of the gonadal layer of that group being slightly over 1.0 mm. (Fig. 1). Two other groups of oysters collected from the stations located at depths of 20 and 30 feet showed the thickness of the gonadal layer as about 0.9 and 0.8 mm. respectively. In all groups, especially in that of the deep water stations, there were individuals whose gonads only recently had changed from the wintering stage, and whose gonadal layer was extremely thin. Later in June the increase in the thickness of the gonadal layer of all three groups of oysters became quite rapid, and early in July, before the beginning of spawning, the gonads reached their maximum development.

Throughout the prespawning period the oysters of the more shallow stations possessed a heavier layer of spawn than the oysters from deeper water (Fig. 1). This difference became more apparent as the season

progressed toward the commencement of spawning. On July 2 the thickness of the gonadal layer of shallow water oysters was approximately twice that of oysters from the 30-foot depth. Oysters of medium deep stations occupied a position between the extremes.

Because the last measurement of gonads during the prespawning period was made on July 2, approximately one week before the beginning of spawning, it must be assumed that during that last week a further increase in thickness of the gonadal layer occurred. Therefore, it is probable that the maximum thickness of the gonadal layer of the oysters at all three depths was greater than is shown in Figure 1. However, judging by the examination of unspawned individuals collected on July

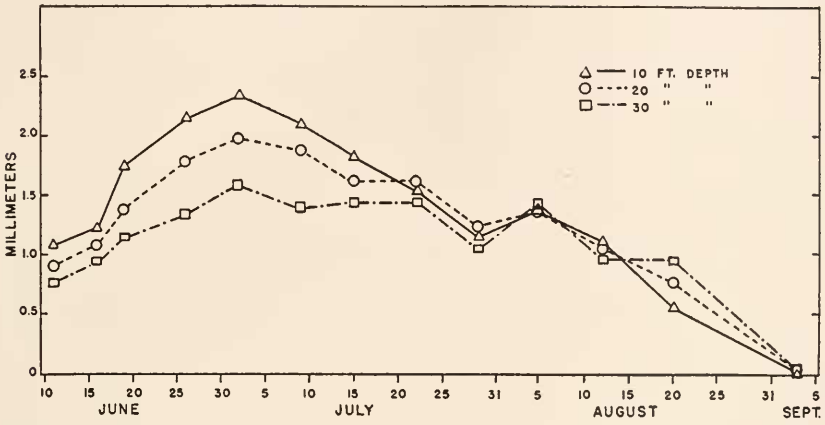

Fig. 1. Mean thickness of the gonadal layer of the oyster at three different depths.

9, the increase in thickness of the gonadal layer during the week elapsing between July 2 and 9 was very small.

In 1941, the beginning of spawning of the oyster population occurred about July 9. Spawning was of a general nature taking place at all the stations regardless of depth. After the beginning of spawning the thickness of the gonadal layers of oysters at all the depths began to decrease. While such a decrease was rather slow and gradual, it was most pronounced in the case of the shallow water oysters (Fig. 1). This, of course, indicated that the shallow water group discharged the spawn in larger quantities and more rapidly than the oysters of deeper water. As a result of the uneven rate of the discharge of spawn, the thickness of the gonadal layers of the oysters of all three depths became actually the same by July 22. Later on, the shallow water oysters began to possess less spawn than the two other groups (Fig. 1).

On July 15, several days after the beginning of spawning, a series of observations on the condition of gonads of the oysters was begun. It was found that the majority of the oysters at all the stations had already released part of their sex cells. It was of interest to note that, contrary to expectations, there were fewer ripe-but-unspawned oysters at the deep water stations than at more shallow ones (Fig. 2*A*). In all cases, nevertheless, the majority of oysters examined at this date were in the less-than-half spawned stage. Such animals constituted 71.0, 61.7 and 81.3 per cent of the samples collected at depths of 10, 20 and 30 feet respectively (Fig. 2*B*). More-than-half spawned oysters were most numerous at the 20-foot depth where they constituted 18.3 per cent of the total number of oysters examined (Fig. 3*C*). Completely spawned oysters were absent in the samples collected at medium-deep and deep stations, but at the shallow stations 1.6 per cent of oysters were identified as entirely spent (Fig. 3*D*). This observation indicated that among the oyster population living in shallow water there was a small group of individuals whose spawning season lasted but a single week. Several oysters of this type were prepared for histological examination which showed by the shrinkage of the gonadal follicles, phagocytosis, and the invasion of the cells of the vesicular connective tissue into the intrafollicular spaces that their gonads were in the typical post-spawning stage.

Within two weeks after the first examination, ripe-but-unspawned oysters showed a marked decrease in numbers. Such a decrease was noted at all three depths (Fig. 2*A*). Nevertheless, unspawned individuals were found in the samples collected at the 10-foot depth until August 12, and at the two greater depths until August 20. However, between July 29 and August 20, ripe-but-unspawned oysters never constituted more than 2.6 per cent of the population at any depth.

Early in August, approximately 50 per cent of the oyster population had half its spawn already discharged (Fig. 4). Again it was noted that the shallow water oysters, living at the 10-foot depth, reached this stage several days earlier than the animals living in deeper water (Fig. 2*B*).

As is shown in Figure 2*B*, the half-spawned stage was reached by the oyster population sometime between August 5 and 12. To determine a more exact date for the midpoint of the spawning period, the following method was employed: the oysters composing ripe-but-unspawned and less-than-half spawned classes were combined in one group, while two other classes, in a more advanced condition, were taken as the second group. By employing such a classification all oysters were divided into two groups of which the first contained all less-than-half spawned

oysters, while the second group was composed of the individuals which had more than half their spawn already discharged. The last group, of course, included all completely spawned oysters. When the percentage of these two groups was plotted against the time, two curves intersected at the point corresponding to August 8 (Fig. 4). Therefore, it can be assumed that this date represents the midpoint of the spawning season or, in other words, the date at which the oyster population of the Sound had discharged approximately one-half its spawn.

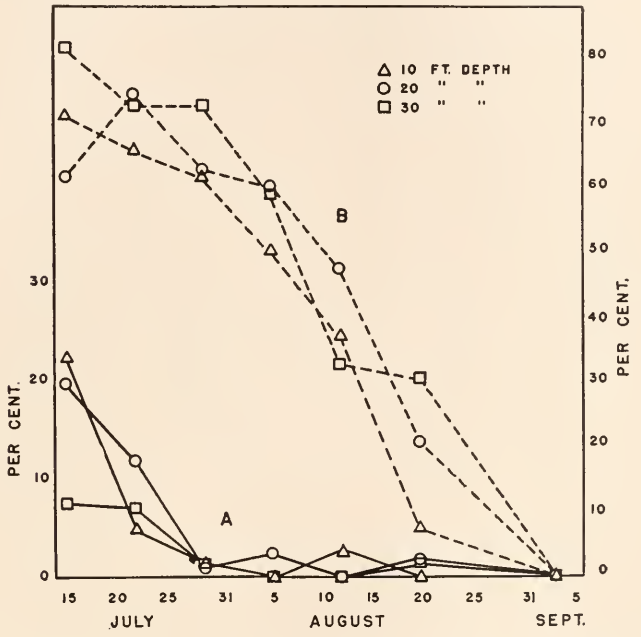

FIG. 2. Percentage of ripe-but-unspawned (*A*), and less-than-half spawned (*B*) oysters at each of three depths.

The conclusion that the midpoint of the spawning season lies close to the date of August 8 is further supported by the data obtained from the measurements of the thickness of the gonadal layer of oysters (Fig. 1). These measurements showed that the average thickness of the gonadal layer of the oysters recorded several days before the beginning of spawning was about 2.0 mm. On the other hand, the average thickness of this layer, as determined on August 12, the date nearest to August 8, was only about 1.0 mm., or approximately one-half that at the time of the maximum development.

Individual oysters containing more than half the spawn were still quite numerous in the samples long after the midpoint of the spawning period was reached (Fig. 2*B*). Even as late as September 20, 32.5 per cent of the oysters living at the depth of 30 feet was found in this stage. At more shallow stations their numbers were smaller.

As was stated before, few completely spawned oysters were found in the samples as early as July 15. Those animals, however, came from

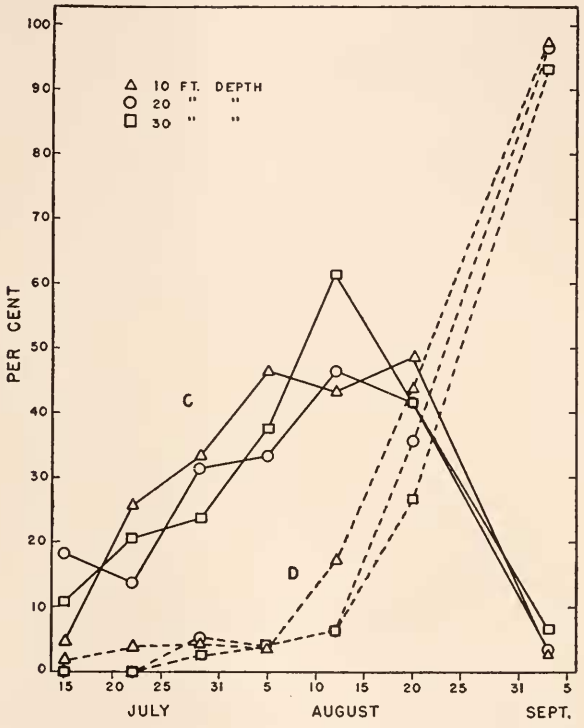

Fig. 3. Percentage of more-than-half spawned (*C*), and completely spawned (*D*) oysters at each of three depths.

shallow water. At deeper stations located at the 20- and 30-foot depths, completely spawned animals were first found on July 29 or two weeks later than at the shallow stations. At that date their numbers were comparatively small and never constituted more than 5.1 per cent of the entire population (Fig. 3*D*). A significant increase in the numbers of completely spawned oysters of shallow water was noted by August 12, when they constituted 17.1 per cent. At the two other depths, large numbers of spent oysters were observed one week later, when they constituted 35.8 and 26.6 per cent of the population living at 20- and 30-foot

depths respectively. After August 20, the number of completely spawned oysters rapidly increased and on September 3, at the end of the observation period, over 95.6 per cent of the entire population belonged to that group (Figs. 3 and 4). The remaining 4.4 per cent represented the animals still containing small quantities of spawn and, therefore, considered as more-than-half spawned but not entirely spent. It may be

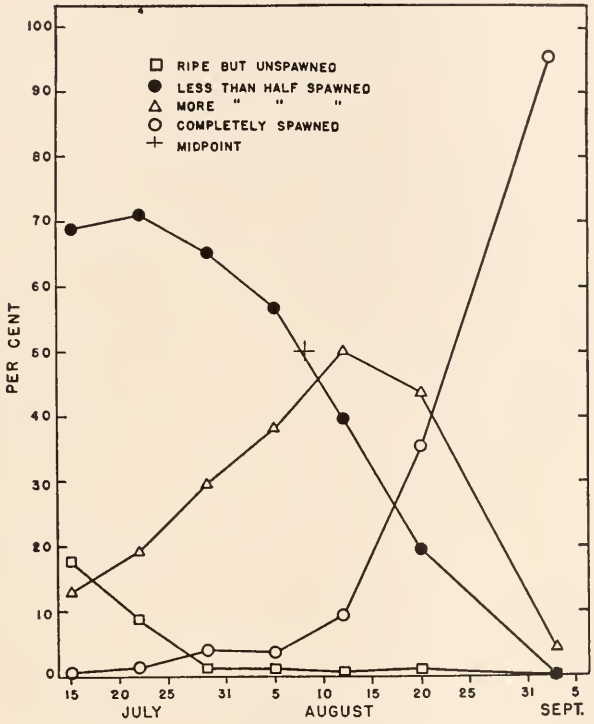

Fig. 4. Percentages of ripe-but-unspawned, less-than-half spawned, more-than-half spawned, and completely spawned individuals composing the oyster population of the depths ranging from 10 to 30 feet. July 15 to September 3, 1941. Cross sign (+) indicates the midpoint of the spawning season.

concluded, however, that the spawning activities of the majority of the oyster population living at the depths ranging from 10 to 30 feet were finished about September 3.

Discussion

The observations conducted in 1941 in Long Island Sound indicated that, within the depth range of from 10 to 30 feet, the spawning of the oyster population began at the same time. This observation is in agree-

ment with those of previous years when it was found that the oysters of shallow and deep water beds approached ripe conditions and discharged spawn on or about the same date (Loosanoff, 1939; Loosanoff and Engle, 1940). The spawning season continued from about July 9 until about September 3. The shallow water oysters finished spawning somewhat earlier than the oysters living in deeper water.

It was determined that the midpoint of the season, or the date by which the oyster population had discharged approximately one-half the spawn accumulated, was reached by August 8. Again shallow water oysters reached this point several days earlier than the animals living in deeper water.

It is of interest to know that, among the oyster population studied, there was a small group found whose spawning activities were begun and ended within a week's time. It is possible that these individuals represent a race physiologically different from other local oysters whose spawning periods extend about two months. It has been suggested that such individuals are the descendants of the oysters brought on several occasions to Long Island Sound from northern waters where the spawning season is of very brief duration.

The presence of ripe-but-unspawned oysters, encountered in the samples collected six weeks after the beginning of the spawning season, presents an interesting problem. The failure of some individuals to spawn until very late in the season was first noticed during the spawning season of 1937 (Loosanoff and Engle, 1940). Physiological ripeness of such a late-spawning type of female oysters was established by fertilizing their eggs with spermatozoa taken from the males of the same late-spawning group. Therefore, it appears that under natural conditions some of the ripe oysters cannot be induced to spawn by a relatively high temperature and by the chemical stimulation caused by the presence in the water of the sex products discharged by the oysters living nearby. These field observations are supported by the laboratory experiments of Galtsoff (1940) who found that from 5.4 to 22.8 per cent of males and from 4.7 to 29.4 per cent of females could not be induced to spawn by the combination of thermal and chemical stimuli. Histological examination of these animals showed that a great majority of them was ripe.

The observation that the oysters living in shallow water develop much larger quantities of spawn than the oysters of greater depths is of considerable significance. It indicates that during the prespawning season it may be advantageous to have large numbers of oysters concentrated in relatively shallow water. In that case, theoretically, each oyster would produce about twice as many sex cells as it would if it were kept

at the depth of 30 feet. At present no satisfactory explanation can be offered as to why the shallow water oysters accumulate larger quantities of spawn. At first the difference in water temperature was suspected as causing much more favorable conditions of existence for shallow water individuals. Field records showed that during the prespawning period, the bottom water temperature at shallow stations was from only 1° to 2° C. higher than at the 30-foot depth. Therefore, even if the difference was actually insignificant, the assumption could be made that the shallow water oysters accumulated more spawn because they lived in warmer water. Such an assumption, however, would be contradictory to the observations of the last nine years which showed rather conclusively that the quantity of spawn developed by oysters in different years could not be correlated with the deviations of temperature during spring and early summer above or below normal (Loosanoff and Engle, 1940). Furthermore, minor differences in temperature have been found to be unimportant in other physiological activities of oysters. For example, Galtsoff (1928), in well controlled experiments performed on a large number of oysters, found that within temperature limits ranging from 13° to 22° C. there was no visible effect of temperature on the opening and closing of shells. Recent experiments on the feeding of oysters conducted by the authors at Milford Laboratory failed to show that, within the temperature range mentioned above, there was a well defined decrease or increase in the rate of feeding of oysters when the temperature of the water was changed by one or two degrees.

The differences in the salinity of the water at the stations of the three different depths were rather small seldom exceeding one part per mille. Evidently such a difference was not significant enough to cause much heavier development of the gonad material in the oysters living at one of the depths. It is thought, therefore, that some other conditions are responsible for the accumulation of greater quantities of spawn by shallow water oysters. The suggestion is offered that it may be due to the presence of larger numbers of food organisms in the shallow zones. Unfortunately the present knowledge of the feeding habits of oysters is rather limited. Even though there are many articles describing the plankton organisms found in the oyster's stomach, little is being said in these articles on the digestion and assimilation of such forms. As a result, very little information is available as to the quantities and qualities of various food organisms assimilated by oysters. Therefore, this phase of the biology of the oyster is not clearly understood. Obviously, in order to ascribe the greater gonad development of oysters of certain depths to their feeding habits and the presence of certain food organisms, further research along these lines is necessary. At present a number of

experiments and observations devised to provide the possible answer to such problems are being conducted at the Milford Laboratory.

Summary

1. Prior to spawning the thickness of the gonadal layer of shallow water oysters was approximately twice that of the oysters living at a 30-foot depth.

2. The spawning of oysters at all depths began on and about July 9.

3. The shallow water oysters discharged spawn in larger quantities and more rapidly than the oysters of deeper water.

4. Among the oyster population living in shallow water there was a small group of individuals whose spawning was completed within a week.

5. Ripe-but-unspawned oysters were found in the samples collected as late as six weeks after the beginning of the spawning season. This indicates that some of the ripe oysters, living under natural conditions, cannot always be induced to spawn by a relatively high temperature and or by the chemical stimulation caused by sex products discharged by the oysters living in the immediate vicinity.

6. Approximately 50 per cent of the oyster population had half its spawn discharged by August 8. This date, therefore, is considered as the midpoint of the spawning period. Shallow water oysters reached the half-spawned stage several days earlier than the deep water individuals.

7. The spawning activities of the oyster population, living at depths ranging from 10 to 30 feet, were finished about September 3. The majority of the shallow water oysters completed their spawning somewhat earlier than those of deep water.

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